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Revision of the pantropical genus *Treptopale* (Annelida: Phyllodocida: Chrysopetalidae): redescription of *Treptopale rudolphi* Perkins, 1985 and description of two new species including comparison of *Treptopale* populations in northern Australia

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ABSTRACT

The monotypic genus *Treptopale*, originally described from the Atlantic Ocean, is now extended – with the description of two new species with a broad and almost sympatric distribution – throughout the Indo-Pacific Ocean. The type species, *Treptopale rudolphi* Perkins, 1985, is redescribed from additional material from the type locality in the Florida Keys, western Atlantic Ocean, and from material examined from the Cape Verde Islands and Cape Town, South Africa. The morphology of the notochaetal lateral paleae group separates the Atlantic *Treptopale rudolphi* from a cryptic *Treptopale* species complex that extends from the Seychelles, western Indian Ocean, throughout the western Indo-Pacific to Hawai'i, eastern Pacific Ocean. Morphological analysis of tropical northern Australian populations of the two new *Treptopale* species, which are typically found among *Halimeda* algae on coral reefs, revealed two species separated primarily on the shape and insertion point of a transitional lateral palea and a marked difference in the degree of raised ribs of the main paleae: *Treptopale homalos* sp. nov. is predominantly found along the eastern Queensland coast from Heron Island north to New Guinea; *T. paramolos* sp. nov. is predominantly found along the Northern Territory coast. The two species occur sympatrically in a number of localities across tropical northern Australia and both are present on offshore and mainland reefs of northern Western Australia. Reproductive and larval states and chaetal patterns within and between species are presented. The two patterns of morphology and diversity present in these taxa, observed also across the Indo-Pacific, are plausibly related to ancient colonisation histories.

KEYWORDS: Annelida, Polychaeta, Chrysopetalidae, *Treptopale*, cryptic new species, coral reefs, taxonomy, systematics, larval morphology, biogeography.

INTRODUCTION

The Chrysopetalidae is one of the most common families of polychaete worms associated with habitat complexity in tropical embayments and fringing mainland and offshore coral reefs of the Indo-Pacific and Western Atlantic (Peyrot-Clausade 1974 [Tulear reefs, Madagascar]; Hutchings & Murray 1982 [Great Barrier Reef (GBR), north-eastern Australia]; Bailey-Brock 1995 [Western Pacific]; Peyrot-Clausade 1976 [Tiahura reefs, Moorea]; Perkins 1985 [Gulf of Mexico, Florida, Caribbean]). In common with many coral reef dwelling polychaetes, chrysopetalids find refuge in algal cover overlying a hard substratum (Bailey-Brock 1980).

Throughout the Indo-Pacific, adults of the chrysopetalid genus *Treptopale* are commonly collected from dead coral rubble often associated with calcareous algae of the genus *Halimeda*. *Treptopale* are small, highly fragmentable chrysopetalids with elongate bodies and translucent to pale golden fans composed of symmetrical paleae held in tight fans over the dorsum. *Treptopale* species have separate sexes and adults are also recorded from the plankton (Watson Russell 2000a).

Treptopale was first listed as part of the Australian chrysopetalid fauna by Watson Russell (2000a). The *Treptopale* species complex was subsequently collected from habitats ranging from algae and rubble in clear deep water from the edge of the continental shelf of the outer Great Barrier Reef, Queensland and Scott Reef, Western Australia, to shallow muddy mainland reefs with high turbidity in Darwin, Northern Territory, to fringing reefs of Ningaloo, Western Australia.

Analysis of the *Treptopale* species complex from tropical northern Australia revealed two morphotypes, based primarily on shape and insertion point of a single transitional lateral palea (labelled subunit 1 palea) and a related marked difference in the degree of ornamentation of the raised ribs on the main paleae. The 'robust' morphotype (designated in 'type 1') was predominantly found along the eastern Queensland coast from Heron Island north to New Guinea, and the more 'fragile' morphotype (designated 'type 2') predominated along the Northern Territory coast. Type I

and type 2 morphotypes were present either sympatrically or separately from offshore and mainland reefs of northern Western Australia.

Similar 'robust' and 'fragile' morphotypes were also found throughout the Indo-Pacific Ocean from similar coral reef habitats. In this paper, on the basis of morphological observations, these morphotypes are interpreted as separate species and are described herein as new species.

MATERIALS AND METHODS

Additional *Treptopale* material from five northern Australian localities was collected for molecular work (Fig. 10). These specimens are marked with an asterisk after the museum registration number in the Material examined sections below. Tissue samples are being analysed using the markers, cytochrome c oxidase subunit 1 (CO1) of mitochondrial DNA (mtDNA) and histone 3. These results will be presented in a separate paper (Wei & Watson in prep.).

Setal terminology follows that of Watson Russell (1986) with designations of notochaetal paleael types based on position: i.e. lateral group inserts below the acicula; main group inserts above the acicula; and median group inserts at the mid-dorsal line. The category 'subunit 1 palea' used in this paper refers to one or two small paleae that insert between the lateral and main groups. Description of species is based on the holotype with numerical data derived from additional material in brackets.

Abbreviations. Within Material examined sections, additional information is included: E, entire specimen; NE, specimen not entire; L, length; W, width. Note that many collections are composed of 'fragments' only.

The material examined for this study is housed in the following institutions: Muséum National d'Histoire Naturelle, Paris (MNHN); Zoological Museum Berlin (ZMB); National Museum of Natural History, Washington (USNM); Australian Museum, Sydney (AM); Museum Victoria, Melbourne (NMV); Museum and Art Gallery of the Northern Territory [formerly Northern Territory Museum], Darwin (NTM); Queensland Museum, Brisbane (QM); Phuket Marine Laboratory, Thailand (PML); Bereniee P. Bishop Museum, Honululu, Hawai'i (BPBM). Other acronyms used in the paper are Australian Institute of Marine Science (AIMS), Charles Darwin University (CDU) and Great Barrier Reef (GBR).

SYSTEMATICS

Family Chrysopetalidae Ehlers, 1864
Treptopale Perkins, 1985

Treptopale Perkins, 1985. Gender masculine. Type-species, by monotypy, *Treptopale rudolphi* Perkins, 1985. Recent, Florida, USA.

Diagnosis. Body elongate, tapering at anterior end; body segments very fragmentable. First segment achaetigerous with 2 pairs of tentacular cirri. Second segment biramous with notochaetae, pair of dorsal cirri; neuropodium with neurochaetae, ventral cirri absent. Mid-body notopodia with lateral, main and median paleae types. Main paleae symmetrical, robustly to minimally ornamented with raised ribs. Lateral paleae blunt-tipped, almost rod-like, with marginal serration absent to minimal, low number of ribs or pointed with distinct margin serration and higher number of ribs. Subunit 1 palea small, pointed or larger, robust with equal margins or fragile with unequal inner margin. Mid-body neurochaetae falcigerous. Pygidium quadrate with two anal cirri.

Description. Maximum segment number 120; segments broadly rectangular in section. Body colour in live animals pale yellow to white, often with bright yellow or orange internal notopodial and neuropodial pigment spots; opaque white patch very common interramally (under compound microscope light looks black in gametogenic individuals). Greenish black algal material may be present in gut; oil droplets common in parapodia. Translucent to pale golden paleae in transverse row on notopodium with leading edges visible distally; median paleae interlock at mid-line forming slight convex median ridge.

Prostomium small, rounded, often compressed between anterior 3 segments. Eyes 2 pairs, violet to red; anterior pair larger and often fused in part to posterior pair. Single, large, distally swollen median antenna and 2 slightly longer lateral antennae, basally swollen and distally cirriform, insert on anteroventral margin of prostomium. Palps 2, ovoid, insert on ventral edge of prostomium. Proboscis eversible with 2 slender stylets with slightly darker distal tips; mouth flap small, usually triangular when relaxed; when contracted, a swollen glandular ridge. Dark pigment spots may be present on mouth fold and surrounding area. Glandular nuchal fold present; visible in varying degrees, capable of covering posterior half of prostomium.

First segment reduced, achaetigerous, supporting 2 pairs of dorsal and ventral tentacular cirri; ventral pair originate adjacent to palps. Second segment biramous, with notopodial fascicle with 3–5, short, almost symmetrical paleae; neuropodium with fascicle of spinigerous neurochaetae; dorsal cirrus present, ventral cirrus absent. Third segment, fused in part with segment 2, directed anterolaterally. All subsequent setigers directed laterally.

Mid-body notopodium with 2–3 (6) slender, subacicular lateral paleae including blunt-tipped, almost rod-like laterals with 1–2 ribs and marginal serration absent to minimal (Atlantic species) or pointed with 3–6 (8) ribs and marginal serration mostly developed (Indo-Pacific species). Symmetrical subunit 1 paleae number 1–2 with serrate margins. Within posterior 10 segments, subunit 1 palea often replaced by much shorter, slim palea with low number of ribs. Small, short, notosetal spines may be present in lateral-anterior position of main paleae group.

Mid-body notopodium with symmetrical (to sub-symmetrical) main paleae, numbering 10–16 (20), with very shallow to short apical points; possess 14–21(23) ribs with variable raised rib pattern, highly sculptured with 2–3 major and nearly every other rib highly ornamented or with 2–3 major and some other ribs either highly or finely serrate or no major ribs and very little to no ornamentation. Main paleae with broad to more rounded distal ends, both margins either robustly or finely serrated. Most-medial main palea more rounded distally, more slender, with fewer number of ribs.

Mid-body notopodium with 3–4 (5) median paleae arising from similar insertion point, comprising 2 taller, broader more laterally positioned paleae and 2 shorter more medial paleae. Possess 9–15(17) internal ribs with 1–3 major and sometimes additional raised and finely to coarsely serrated ribs (that extend part or full length of palea) to minimal ornamentation. Median paleae range from usual broad and asymmetric to slender, just sub-symmetrical shape. Apices of all paleae types may be covered in minute hoods. Dorsal cirrostyle subulate, strongly to weakly pseudoarticulated, inserting at lateral posterior edge of notopodium. Interramal region ciliate.

First chaetigerous neuropodium with all spinigerous neurosetae; setigers 2–5 with 1–2 spinigers and long-bladed falcigers. Mid-body broad, pointed neuropodium with single long acicula below which insert fascicle of heterogomph neurochaetae; superior group of 1–3 serrate, long-bladed falcigers, mid-group with about 20 falcigers with medium length serrate blades, inferior group with about 6–8 falcigers with shorter slender blades with fine dentition; narrowest blades found in posterior setigers. All neurochaetal shaft cores subdivided internally with longitudinal and horizontal striae. Ventral cirrus short and broad to more filiform, weakly pseudoarticulated, inserting below neurosetal fascicle. Pygidium quadrate, with 2 filiform anal cirri on posterolateral edge. Anus ventral.

Remarks. The majority of chrysopetalid palcate genera (e.g. *Treptopale, Arichlidon, Bhawania* and *Paleaquor*) comprise cryptic species that are morphologically difficult to separate (pers. obs.). Complexes of cryptic species of these genera have, on close inspection, subtle morphological differences, often based on the presence and shape of a single paleal notochaeta. It is these single palea that insert 'between' the main paleae groups that turn out to be a key species character e.g. subunit 1 palea in *Treptopale* and medial-most main palea in *Arichlidon* (Watson Russell 1986, 1998, 2000b).

Day (1962: 635) incorrectly synonymised *Paleanotus* with *Chrysopetalum*. Both genera are clearly distinguished not only by the very characteristic notochaetal types but by differences of the anterior end. Perkins (1985: 865) recognised these two genera as distinct and further created two new genera, *Treptopale* and *Hyalopale*, closely related to *Paleanotus* as they share the same anterior end configuration as well as similarities of chaetal types. Species of *Treptopale* are distinguished by predominantly symmetrical main paleae, whereas *Paleanotus* possesses asymmetrical main paleae, as does the very small and rarely occurring *Hyalopale*, which possesses a number of paleanotine neotenous characters. Perkins (1985) did not observe the *Treptopale* pygidium, but its quadrate shape with two small anal cirri (Fig. 8B) is the same as that of *Paleanotus* and *Hyalopale* (pers. obs.).

Perkins (1985) stated that *Treptopale* differs from *Paleanotus* in two characteristics – the position of the mouth opening related to possible differences in the structure of the proboscis, and the overall number of body segments. According to the author's present research there are no structural proboscidial differences between these two genera. The position of prostomium and its appendages plus that of the mouth fold changes according to the degree of contraction of the anterior end within the anterior segments. When the anterior end is contracted tightly, the prostomial appendages are hardly visible dorsally and better viewed in ventral position (Fig. 6B), but when more relaxed they are more visible in antero-dorsal view (Fig. 4A). When contracted, the mouth fold appears as a triangular structure immediately below the palps near chaetiger 1 and 2 boundary (Fig. 6B). When the mouth is more open, it can appear as a horizontal or longitudinal gash at a level between chaetiger 2 and 3, with the revealed lips covered in dark glandular spots, which may also be seen on the surrounding ventrum (Fig. 6C). Perkins (1985) recorded entire specimens of *Treptopale* reching 60 segments and *Paleanotus* to 40 segments. Material recorded in this paper and observed by the author increases the former to 120 segments and the latter to 60 segments.

Treptopale does not possess a discreet rounded caruncle, as in *Chrysopetalum*, but a glandular nuchal fold. This fold is also present in *Paleanotus* and in most other chrysopetalid genera. Perkins (1985) described *Treptopale* as having no caruncle, but in both Atlantic and Indo-Pacific specimens where the prostomium is not fully contracted, a glandular nuchal fold is clearly evident (Fig. 6A). However, *Treptopale* does have greater narrowing of the anterior segments compared to other genera and, while a glandular nuchal area is always visible, a discrete nuchal membranous fold is sometimes not visible.

The insertion points of the notochaetal paleae types and the numbers of lateral, main and median paleae, including their rib numbers, are similar between *Treptopale* and *Paleanotus*, as also are the shapes of the dorsal and ventral cirri, with the dorsal cirri often sharing the same characteristic downward 'hang' (Figs. 1A,C).

Treptopale differs from *Paleanotus* in the possession of symmetrical paleae and uniquely shaped subunit 1 palea(e); the longer body has an anterior end comparitively narrower and body segments more fragmentable. The three *Treptopale* species described in this paper are all more similar to each other in comparison to a much larger suite of clearly morphologically differentiated species of *Paleanotus*. A

paper on *Paleanotus* is currently in preparation by the author, including DNA sequences, the results of which will help to clarify relationships between these two genera.

At first glance, it can be easy to confuse *Treptopale* (especially *T. homalos* sp. nov) and species of the genus *Arichlidon* in their possession of ornate symmetrical main paleae. However, *Treptopale* lacks the dense granules of the main palcae seen in *Arichlidon.* Both genera have different body shapes, that of *Arichlidon* being much broader throughout its length and its paleae often being flecked with a brown scale. The small lateral fascicle in *Treptopale* is distinct and separate with slender, short palcae in comparison to the broad lateral fascicle of *Arichlidon* which forms a smooth intergrading fascicle with the main group (Watson Russell 1998).

Treptopale and the rarely occurring *Bhawania riveti* (species complex), can co-occur in the same coral rubble habitat, and both have similarly shaped lateral, symmetrical main and median palcae. However, *Treptopale* is associated with *Halimeda* and rubble, and *Bhawania riveti* lives deeper, inside cavities in coral blocks. The body form and colour of both are very different: *Treptopale* has a pale body with silvery to pale golden paleae fans and up to 120 segments, whereas *B. riveti* has a brown body with dark golden paleae fans, ventral dark brown interramal spots and is overall more slender, with up to 300 segments.

Habitat and Distribution. Members of the genus *Treptopale* are found in the tropical regions of the major continents (pantropical) on mainland and offshore coral reefs between 24°N and 33°S. *Treptopale* species inhabit coral rubble associated with *Halimeda* and coralline algaesor rubble in sand from LWS to 35 m.

Key to species of the genus *Treptopale*

1. Mid-body notopodial subacicular lateral paleae include 2 (3) slender, blunt tipped, almost rod-like, paleae with 1–2 ribs; margin serration absent to minimal .... *Treptopale rudolphi* (Atlantic, Fig. 1A)
— Mid-body notopodial subacicular lateral palcae with 2–4 (6) slender, pointed paleae with 3–6 (8) ribs; marginal serration mostly well developed..... ..... 2 (Indo-Pacific, Fig. 3A)

2. Mid-body notopodia with robust subunit 1 palea (palea between lateral and main groups) inserting supra-acicularly, with symmetrical margins, 6–12 ribs including 1–4 raised ribs; main paleae with robustly ornamented raised ribs..... ..... *Treptopale homalos* sp. nov. (Fig. 3B)
— Mid-body notopodia with less robust subunit 1 palea inserting either overlying or sub-acicularly, pointed with inner margin asymmetrical, 6–11 ribs (including 1–2 finely raised ribs); main paleae with minimal to finely ornamented raised ribs..... ..... *Treptopale paromolos* sp. nov. (Fig.7)

***Treptopale rudolphi* Perkins, 1985**

Figs 1 A–D, 2

Treptopale rudolphi Perkins, 1985: 905–907; Núñez 1998: 21–27.

Holotype (not examined) – USNM 97370, 1E, 60 segments, L: 5.5 mm, W: 0.5 mm, Western Atlantic, United States, Florida, Ragged Keys, 25°32'N, 80°10'W, 2–3 m, hard substrate (data from Perkins 1985).

Material examined. WESTERN ATLANTIC OCEAN: USNM 1148243, anterior end, 3 sets fragments, W: 0.72 mm, United States, Florida, Mud Key, 24°42'N, 81°45'W, coll. Cr. 17, R.V. *Hernan Cortez*, April 1965; MNHN PNT 25, fragments, W: 1.4 mm. EASTERN ATLANTIC OCEAN: Cape Verde Islands, Stn. 52, rocky bottom, 20 m, coll. R.V. *Calypso*; ZMB 5763, anterior end, mid-body fragments, 40 NE, W: 1.2 mm, South Africa, Cape Town, Simonstown, coll. Deutsche Südpolar Expedition, July 1903; SAM 21453, fragments, W: 1.4 mm, South Africa, Seal Island.

Description (based on composite of fragmented material). Body elongate, pale yellow; palcae pale golden to almost transparent, in uniform rows down dorsum. Prostomium with 2 pairs of red eyes, short median antenna, 2 filiform lateral antennae, 2 rounded palps; nuchal fold very small, obscured. Segments 1 and 2 with 3 pairs of dorsal and ventral cirri (Perkins 1985: figs 26 A,B).

Mid-body notopodium with 2–3, slender, blunt-tipped, almost rod-like lateral paleae with 1–2 ribs; no marginal serration on lower edge, very slight serration on upper margin (Fig. 1 A–D). Subunit 1 palcae, numbering 1–2, with serrate margins, 3–5 ribs, pointed distally, no raised ribs (Fig. 1 D). Few small anterior spines present, observed only in Florida individual. Symmetrical main paleae 10–13 with 17–21 (23) ribs and 2–4 lightly ornamented ribs. Three asymmetrical median paleae present with 11–12 ribs (Florida and Cape Verde Islands) and 14–15(16) (Simonstown and Seal Island); 0–3 very lightly beaded ribs (Fig. 1C).

Mid-body neuropodium with 2–3 superior long-bladed falcigers, 3–4 shorter long-bladed falcigers, 8–10 medium-bladed falcigers and 4–6 short-bladed inferior falcigers. Total about 20 (Cape Verde specimen). Pygidium quadrate, with 2 slender anal cirri.

Remarks. Perkins' (1985: 907) original description stated that the lateral palcae of *Treptopale rudolphi* have serrate margins and "about 5 ribs". He did not figure any lateral paleae but did figure "anterior group palea" (Perkins 1985: fig. 27D) which correspond to the subunit 1 palea of this study. It appears that Perkins collapsed the description of the lateral paleae with that of the subunit 1 palea(e). *Treptopale rudolphi* examined from Mud Key, Florida (near the type locality of Ragged Keys) and from three other eastern Atlantic localities, all possess the same morphology of the subacicular lateral paleae fascicle, i.e. blunt-tipped laterals with 1–3 ribs and little or no marginal serration.

The Mud Key specimen has one to two subunit 1 paleae, inserting above the dorsal acicula which are short, possess 4–5 ribs, are pointed distally, and have serrate margins

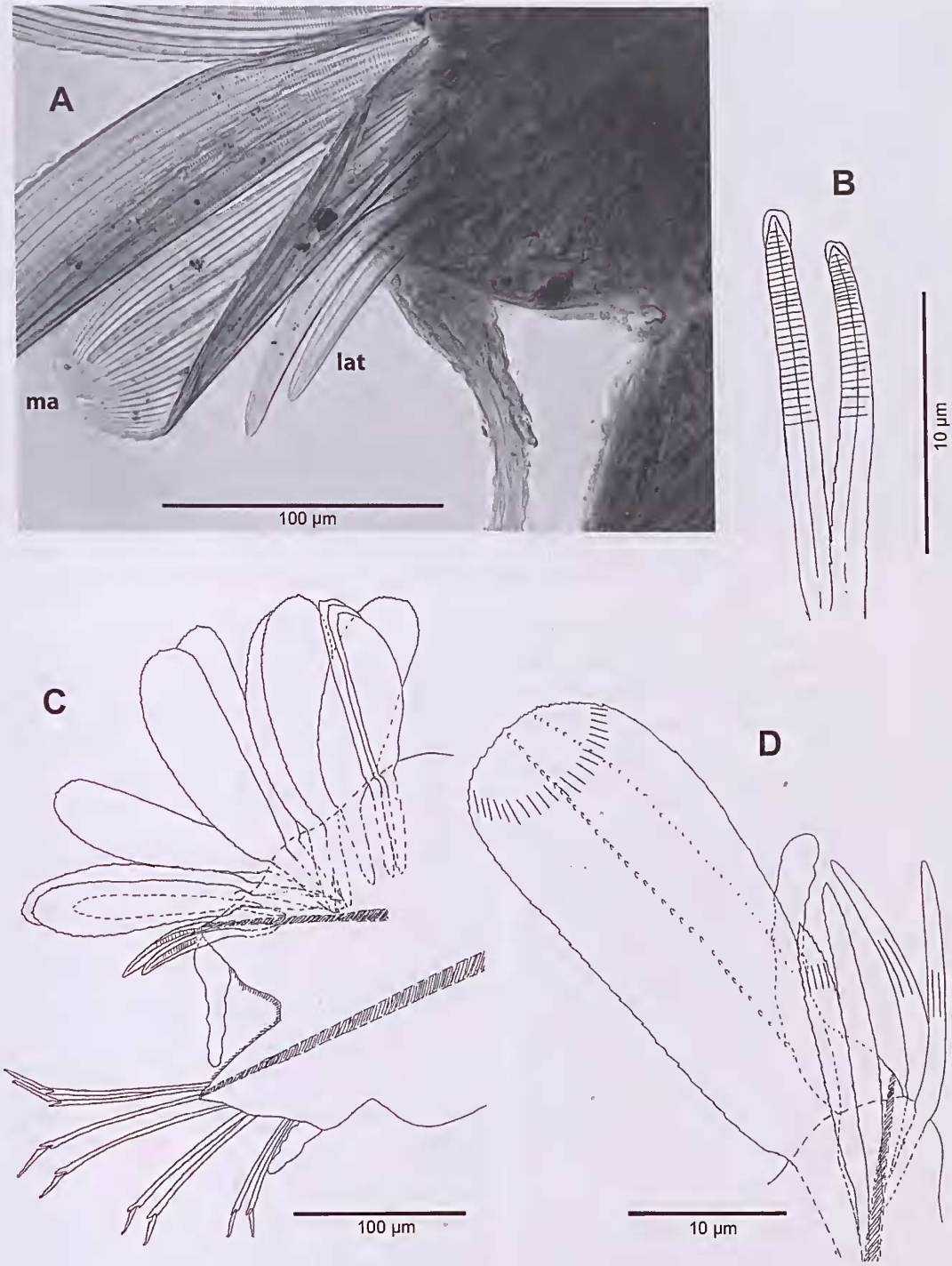

Fig. 1. *Treptopale rudolphi* sp. nov.: **A,C**, ZMB 5763, South Africa, slide preparation, mid-body parapodium, la = lateral paleae, ma = main paleae; **B**, MNHN PNT 25, Cape Verde Islands, detail of lateral paleae mid-body parapodium; **C**, mid-body parapodium with notoehaetal lateral, main and median paleae groups [Note: not all neuroehaetae drawn]; **D**, USNM 1148243, Mud Key, Florida, mid body parapodium, detail of lateral and subunit 1 paleae. Scale lines: A –100 um; B – 0.01mm; C – 0.1mm; D – 0.01 mm.

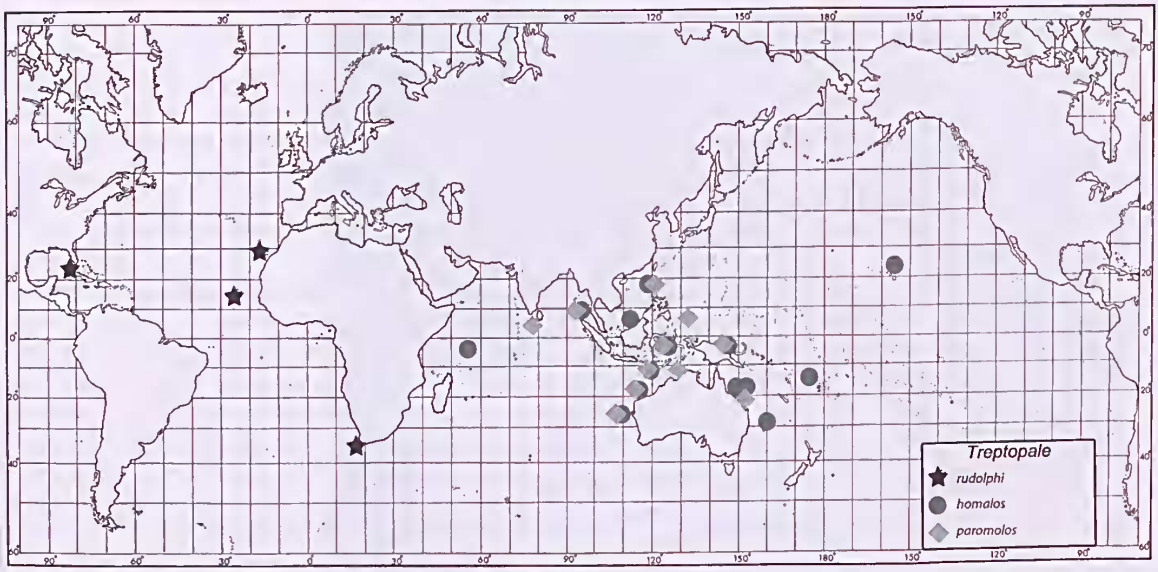

Fig. 2. World map showing distribution of species of the genus *Treptopale*.

(Fig. 1D). The larger Simonstown individual has one subunit 1 palea with 10–11 ribs (Fig. 1C). This latter specimen also possesses lightly ribbed main and median paleae very similar to those seen in the specimens from Florida. The other South African Seal Island specimen has slightly heavier ribbed main paleae. Unfortunately it was not possible to examine the lateral paleae morphology or a small unusual neuropodial structure described for a *Treptopale rudolphi* specimen from the Canary Islands (Núñez 1998: fig 2G, specimen lost, Núñez, pers. comm.).

Detailed morphological examination comparing the very similar Atlantic and Indo-Pacific *Treptopale* material revealed small but consistent differences in the shape and number of the lateral paleae fascicle. The lateral paleae morphology is the most important character separating the Atlantic *Treptopale* species (Fig.1 A–D) from the Indo-Pacific species (compare Figs. 3A, 4E,F, 8A, and see Key). Atlantic specimens also have main and median paleae with none or few very shallow raised ribs (see Perkins 1985: fig. 27; SEM Núñez 1998: fig. 3C; this paper Fig.1 A,D). This degree of ornamentation is closer to that seen in the Indo-Pacific *Treptopale paromolos* sp. nov. and distinct from the highly ornamented Indo-Pacific *Treptopale homalos* sp. nov.

The question of whether *Treptopale rudolphi* is truly an amphi-Atlantic species needs to be tested at the molecular level with a larger sample size. Trans-Atlantic dispersal of meiofaunal polychaetes of the same species has been recorded by Westheide *et al.* (2003) based on evidence from molecular data.

Habitat and Distribution. *Treptopale rudolphi* is found between 24°N (Florida) and 33°S (Cape Town, South Africa), western and eastern Atlantic Ocean. The species is associated with hard rocky bottoms (Perkins 1985) and sponges (Núñez 1998), from 2–20 m.

Treptopale homalos sp. nov.

Figs 2, 3A,B, 4A–F, 10

Material examined. Holotype – QM G232165, 51 segments, entire, L: 7 mm, W: 0.8 mm, Australia, Queensland, GBR, Lizard Island, SW Palfey Island, Stn. CGLI024, 14°41'S, 145°6'E, coral rubble, 4 m, coll. M. Ekins, April 2008. Paratype – NTM W.23074*, 1, Lizard Island, Mermaid Cove, 14°38'S, 145°27'W, Stn.CG LI006, Halimeda & rubble, 2 m, coll. C. Watson, April 2008.

Additional (non-type) material examined. QUEENSLAND: GBR, NTM W. 23221, 2 (1 adult, 40NE,1 post larvae, 10E), off Townsville, inner shelf, Philips Reef, 18°59'S, 146°36'E, coral rubble, coll. M. Riddle, October 1985; NTM W. 23076*, 1, Lizard Island, bommie near entrance to lagoon, 14°41'S, 145°27'W, 15 m, coll. C. Glasby, April 2008; NTM W.23077*, 1, North Direction Island, Stn. CGLI019, 14°44'S, 145°30'W, 5 m, coll. M. Ekins, April 2008; NTM W.22891*, 1E, male, 118 segments, L: 21.2 mm, W: 1.5 mm, Outer Barrier Reef, Hicks Reef, Stn. CWLI020, 14°38'S, 145° 7'E, coral rubble, 2–18 m, coll. C. Watson & K. Mills, February 2009; NTM W.22892*, 1NE, 60 segments, L: 9.6 mm, W: 1.0 mm, ovigerous female, Hicks Reef, Stn. CWLI047, 14°26'S, 145°26'E, 10 m, coll. M. Blazewicz & N. Bruce, February 2009; NTM W.22891*, 1E, 120 segments, L: 21.2 mm, W: 1.5 mm, Day Reef, Stn. CWLI048, 14°30'S, 145°0'E, 30 m, coll. J. Caley & K. Mills, February 2009; NTM W.22889*, 1, Yonge Reef, Stn.CWLI015, 14°36'S, 145°37'W, 2 m, coll. C. Watson, February 2009; NTM W.23055, 1E, Snake Pit, Stn. CWLI054A, 14°40'S, 145°34'W, *Halimeda* compacted banks, 30 m, coll. J. Caley & S. Smith, February 2009; NTM W.22890*, 1, MacGillivray Reef, Stn. CWLI058, 14°39'S,

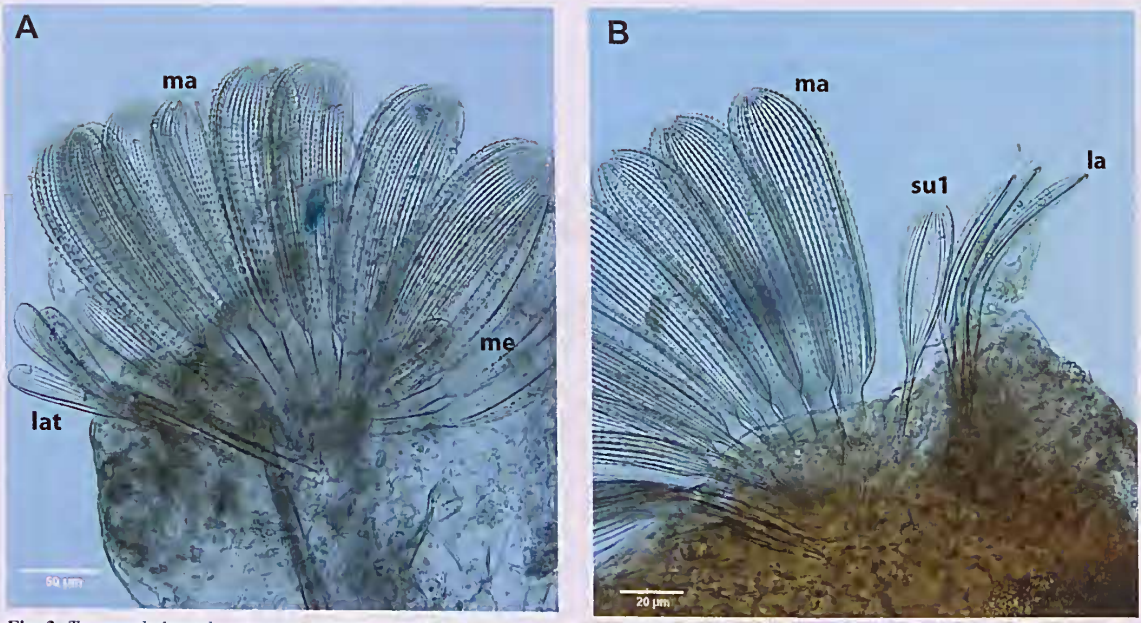

Fig. 3. *Treptopale homalos* sp. nov.: NTM W.22891, Lizard Island, Great Barrier Reef: **A**, slide preparation, mid-body notopodium in part, lat = lateral paleae group, ma = main paleae group, me = median paleae group; **B**, slide preparation, mid-body notopodium in part, su1 = subunit 1 palea.

145°29'W, 30 m, coll. K. Mills & S. Smith, February 2009; NTM W.23058, 1, Linnet Reef, Stn. CWLI027, 14°46'S, 145°20'W, 4 m, coll. M. Blazewicz, February 2009; NTM W.23071*, 1, Heron Island, Capricorn Group, South East Lamont Reef, Stn. HI09-059, 23°35'S, 152°3'E, coarse coral rubble, 15 m, coll. N. Bruce, November 2009; NTM W.23072*, 1, North Wistari Reef, Stn. HI09-002, 23°27'S, 152°52'E, coarse coral rubble, 12 m, coll. M. Capa & P. Hutchings, November 2009; NTM W.23073*, 1, Sykes Reef, Stn. HI09-046, 23°25'S, 152°2'E, coarse coral rubble,10 m, November 2009; NTM W.23070*, 1, Sykes Reef, Stn. HI09-046, 23°26'S, 152°2'E, coarse coral rubble,10 m, November 2009; NTM W.23079, 1, Lamont Reef, Stn. HI09-031, 23°36'S, 152°3'E, coarse coral rubble, 30 m, coll. S. Smith & A. Anderson, November 2009; NTM W.23080, 1, Twin Peaks, Stn. HI09-012, 23°28'S, 152°57'E, 2 m, coarse coral rubble, coll. M. Capa, November 2009. NEW SOUTH WALES: AM W.23356, 1NE, anterior end, W: 0.5 mm, Elizabeth Reef, 29°55'S, 159°01'E, Stn. 43, LWS, from algae, coll. P. Hutchings, December 1987; AM W.23362, 1E, 32 segments, L: 2.6 mm, Elizabeth Reef, Stn.36, coll. P. Hutchings, December 1987. NORTHERN TERRITORY: NTM W. 22944*, 1NE, 49 segments, W: 1.5 mm, Darwin, Channel Island, 12°33'S, 130°52'E, *Halimeda*, brown & red algae, rubble, LWS, coll. C. Watson, September 2007. WESTERN AUSTRALIA: NTM W. 4158, 1E plus fragments, Ashmore Reef, 12°S, 123°E, coralline algae & coral rubble, 15 m, coll. B.C. Russell, February 1984; NTM W.7288, 1NE, 74 segments, male, Cartier Reef, Stn.RH6, outer reef slope, 14 m, coll. J.R. Hanley, May 1992; NTM W.2273, 111NE, W: 1.52 mm, Broome, Cable Beach,17°58'S, 122°11'E, under rocks, LWS, coll. J.R. Hanley, September 1984; AM W.36172, 1NE, Dampier Archipelago, north east Delambre Island, coll. P. Hutchings, August 2000; NTM W.5107, 1, ovigerous female, 85NE, W: 1.7 mm, Exmouth, S.S. *Mildura* wreck, 21°86'S, 114°07'E, inside rubble, LWS, coll. J.R. Hanley, February 1988; NTM W.23082*, fragments, Ningaloo, 22°5'S, 113°61'E, Stn.NR09-004, coarse coral rubble, 17 m, coll. P. Hutchings *et al*., May 2009. WESTERN PACIFIC OCEAN, NEW GUINEA: NTM W.21788, fragments, W: 1.3 mm, Wongat Island, 5°8'N, 145°49'E, Stn. RH91/88, coral reef and sand, 10 m, coll. J.R. Hanley, October 1991; NTM W.21782, 1, Malamal Island, 5°9'N, 147°5'E, Stn. RH91/104, seagrass, sand & coral,1 m, coll. J.R. Hanley, October 1991; NTM W.21786, 1, Padoz Reef, patch reef inside lagoon, 5°9'S, 145°48'E, Stn. RH 91/83, 21 m, coll. J.R. Hanley, October 1991; NTM W.21783, 1, Tripod Reef, Madang, 5°10'S, 145°50'E, Stn. RH 91/108, 8 m, coll. J.R. Hanley, 26 October 1991; AMERICAN SAMOA: AM W.36675, 1, Vatia Bay, 14°14'S, 170°4'E, Stn. 9, 28 m, coll. Reath & Bonito, October 2000. INDONESIA: NTM W.21790, fragments, Flores, Maumere, coral rubble & sand, 24–27 m, coll. B.C. Russell, Nov 1991; AM W.36676, 1, Togian Island, Hut Reef, 0°3'S, 121°41'S, outer reef slope, coralline algae, 35 m, coll. P. Hutchings, September 1999. MALAYSIA, SOUTH CHINA SEA: NTM W.13139, 50NE, Sabah, Kota Kinabalu, Sapi island, 5°58'N, 116°05'E, coral rubble & algae, 1.5 m, coll. C. Watson, August 1995. PHILIPPINE ISLANDS: NTM W.23363, fragments, Luzon, Cape Bolinao, 16°25'N, 119°50'E, coral rubble, sponge, red algae, 12–25 m, coll.

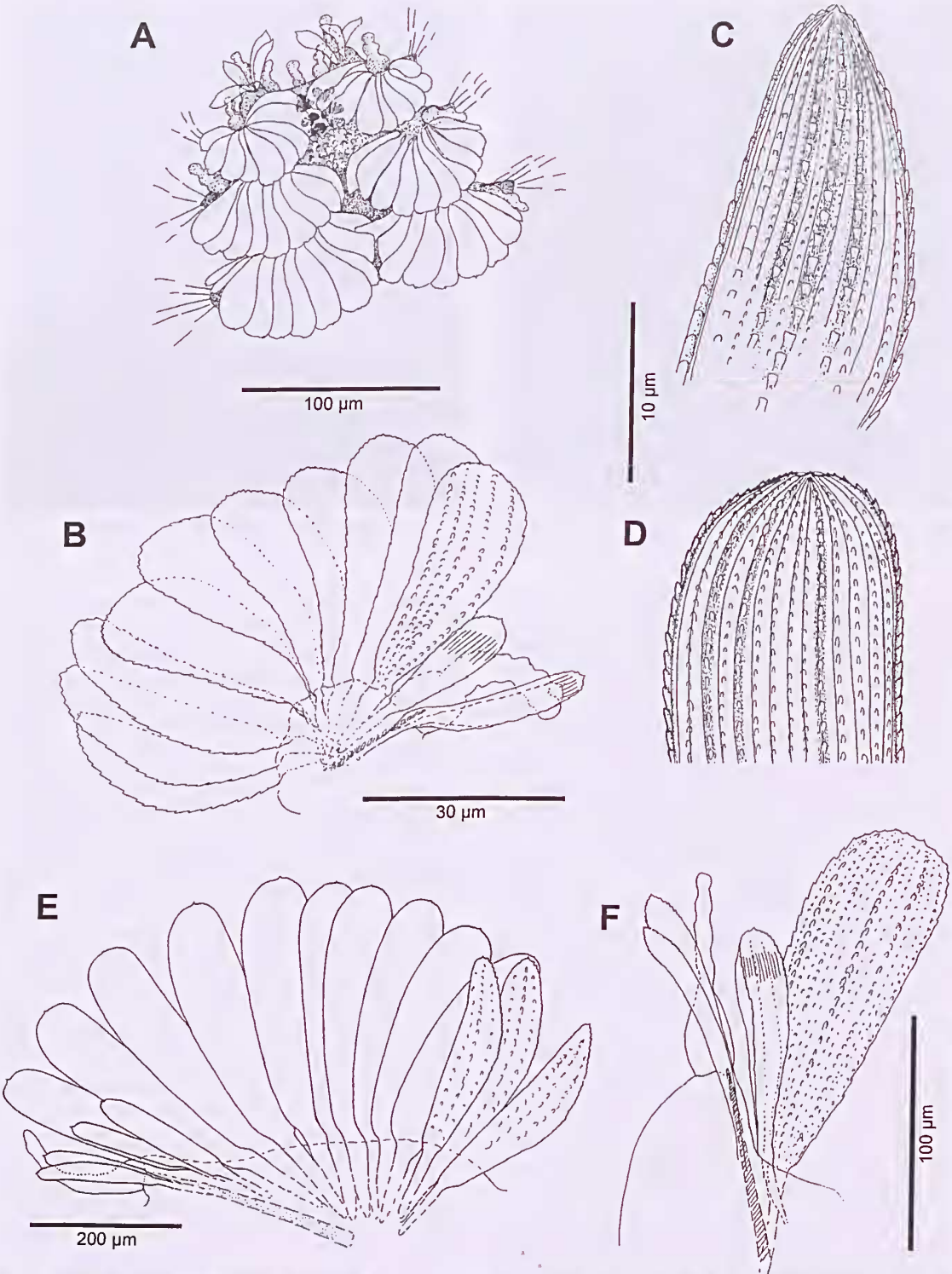

Fig. 4. *Treptopale homalos* sp. nov. **A,B**, Holotype, QM G232165, Lizard Island, Great Barrier Reef: **A**, anterior end, dorsal view; **B**, notopodium, setiger 3; **C,D**, AM W.196779, Lizard Island, Great Barrier Reef, planktonic specimen, **C**, median palea detail, **D**, main palea detail; **E**, MNHN A845, Seychelles, mid-body notopodium; **F**, NTM W. 23225, Hawaii, mid-body notopodium in part. Scale lines: A – 0.1 mm; B – 0.1 mm; C – 0.01 mm; D – 0.01 mm; E – 0.2 mm; F – 0.1 mm.

B.C. Russell, October 1995. EASTERN PACIFIC OCEAN, HAWAI'I: NTM.W.23225, anterior and posterior ends and fragments, Oahu Island, 21°30'N, 158°00'W, Kaneohe Bay, coral reef, shallow, coll. J. Broek; NTM W.23224, anterior & posterior ends, Kaneohe Bay, coral reef, deep, coll. J. Broek. INDIAN OCEAN: THAILAND: NTM W.23359, fragments, Surin Island, 10°N, 98°E, amongst oyster shells, coll. A. Nateewathana & J. Hylleberg, February 1981. SEYCHELLES: MNHN A845, fragments, 4°35'S, 55°40'E, Tanikely, coll. Cherbonnier, April 1960. PLANKTON, ADULT MATERIAL: AM W.196779, 2 midbody fragments, W: 0.72 mm, Osprey Island, Stn.16.7.2, 20.36 hr, 3 m, coll. J. Leis, July 1979; AM W.196780, 1E, 44 segments, L: 4.2 mm, W: 0.7mm, Lizard Island lagoon, Stn.24.7.2, 19.55 hr, 3 m, coll. J. Leis, July 1979. POST-LARVAL MATERIAL: NTM W.17860, 10E, L: 0.64 mm, W: 0.28 mm, Queensland, Dip Reef, 18°25'S, 147°27'E, coll. M. Riddle, October 1985; NTM W.18249, 13E, length 0.6 mm, width 0.32 mm, Lodestone Reef, mid-shelf, 18°42'S, 147°06'E, coll. M. Riddle, October 1985; NTM W.18250, 12E, Philips Reef, inner shelf, 18°59'S, 146°36'E, coll. M. Riddle, October 1985.

Description. Body elongate, white to pale yellow (pale greenish in some live specimens); deep to pale gold paleae in uniform rows covering dorsum. Quadrate-shaped prostomium partly contracted ventrally, with scattered dark maroon-red eye pigment; median antenna short, bulbous distally; 2 filiform lateral antennae with bulbous bases; 2 rounded palps; nuchal fold small, clearly visible glandular area posterior to prostomium (Fig. 4A). Segment 1 uniramous, achaetigerous with 2 pairs of tentacular cirri. Segment 2 (setiger 1) biramous; notopodium with up to 4 short paleae with 4–6 ribs and dorsal cirrus; neuropodium with fascicle of spinigerous setae, ventral cirri absent.

Setiger 2 with lateral and main paleae, no median paleae present. Setiger 3 with 1–2 lateral paleae with 5–6 ribs; subunit 1 palea with with serrate margins, 9 ribs including 2 raised, inserting above dorsal aciculum and at base of lateral main paleae; 7 main with 16 ribs heavily ornamented; 3 broad median paleae (Fig. 4B). Mid-body lateral paleae number 2– 3 (4,5), with 5–8 (9) ribs; subunit 1 numbering 1–2, with 8–12 (13) ribs and 1–4 slightly ornamented ribs (Fig. 3A,B).

Main paleae with heavily ornamented raised ribs present from setiger 2. Mid-body symmetrical main paleae number 10–13 (15) with 15–18 (20) ribs, with up to 18 ribs raised and ornate. Medial-most main paleae slightly more slender and rounded distally; lateral-most main paleae usually robust (Figs. 3A,B, 4 D). Asymmetrical 3–4 robust median paleae with 11–13 (14) ribs with 3–4 major raised ribs and 3–6 minor raised ribs (Fig. 4C, E,F).

Anterior neuropodium with spinigers and long-bladed falcigers; mid-body neuropodium with 2 superior long-bladed falcigers, about 15–20 medium length bladed falcigers, about 6–8 short-bladed falcigers; total about 30 in large specimens. Pygidium quadrate with 2 slender anal cirri.

Remarks. In addition to the two major characters given in the key, *Treptopale homalos* consistently exhibits a number of other characters differentiating it from *T. paromolos*: darker golden paleae; body with a squarer cross section; paleal fans sitting more erect, almost like a 'shelf'; and main and median paleae types with larger serrations on margins (Figs. 3A,B, 4C,D,F). In comparison, *Treptopale paromolos* possesses: silvery to very pale golden paleae; body with a rectangular cross section; paleae fans sitting flatter on dorsum; and main and median paleae types with finer serrations on margins (Figs 7, 8A,E).

Observations on intraspecific variation within *T. homalos* included an atypical long, slender ovigerous female with large eggs from Lizard Island (NTM W. 22892). It exhibited all paleal types with fewer ribs than usual; lateral 3–4, main 10–14, and median more slender, symmetrical with 7–10 ribs and serration not as heavy. A specimen from Heron Island had similar paleal types. Both possessed typical *T. homalos* subunit 1 paleae and, as only two specimens with these lower rib counts were found, they are considered to belong to this species. Specimens of *T. homalos* from the plankton at Lizard Island exhibited a typical morphology (Fig. 4C,D) with no chaetal specialisations.

Entire specimens of 51 segments (Lizard Island) and 71 segments (Heron Island) were dissected to observe changes down the body. Shorter and squarer, heavily ornamented main paleae are evident in anterior setigers, from setiger 2 (Fig. 3B). The mid-body main paleae are similarly ornamented with slightly less ornamentation in the main paleae of posterior 5–10 setigers. Robust subunit 1 palea are present from around anterior setiger 5 to posterior setiger 10 whereafter a slim, short subunit 1 palea is observed in a similar position in the notochaetal fascicle. Lateral paleae are fairly consistent in number throughout the body (i.e. 2–3), but number 4–5 in posterior third of body with larger numbers occurring on some segments very infrequently. Lateral paleae in some Heron Island individuals also had margins with finer to less serration than seen usually.

The author observed that the rarely occurring much larger, broader specimens such as that from the Seychelles had main paleae that were longer, more slender, and more rounded distally (Fig. 3E) compared to those seen in smaller specimens from Hawai'i (Fig. 4F).

The three tiny larval individuals from reefs off Townsville have white bodies dorsally covered with transparent paleae fans, are filled with yolk, possess laeunae with oil in the neuropodia and are similar in shape to the 10 segmented specimen of *Treptopale paromolos* from the Ashmore Reef. Their mid- to posterior-body main paleae have 15 ribs with the majority raised; the lateral main paleae are more slender with 9–10 ribs and 3 raised. There are three broad asymmetrical median with 13 ribs. The degree of ornamentation of main paleae down the body indicates these individuals belong to *T. homalos*. The Philips Reef

benthic post-larva was also in the same collection as adult *T. homalos*. However, there is no sign of the typical *T. homalos* adult subunit 1 palea. The subunit 1 palea present is long, broad and oddly-shaped, a bit like *T. paromolos* but different enough to be questionable.

Habitat and Distribution. *Treptopale homalos* lives among coral rubble often associated with *Halimeda* algae, corallines, seagrass and encrusting sponges in depths from LWS to 35 m. It is known from the western Indian Ocean, Seychelles, commonly recorded in the western Pacific and extends across to Hawai'i in the eastern Pacific. Within Southeast Asia it presently occurs from New Guinea to the Philippines, and within tropical northern Australia from the east coast Elizabeth Reef to Ningaloo Reef on the west coast.

Etymology. The species name *homalos* is a noun in apposition from the Greek meaning 'even' or 'equal' and refers to the equal-sized margins of the robust subunit 1 palea.

Treptopale paromolos sp. nov.

Figs. 2, 5, 6A–D, 7, 8A–E, 9A–C, 10

Bhawania sp. B Hartmann-Sehröder, 1979: 79, figs 11–13.

Material examined. HOLOTYPE – NTM W.23048, 44E segments, L: 7.60 mm, W: 1.2 mm, ovigerous female with large eggs, Australia, Northern Territory, Darwin, Lee Point, 12°18'S, 130°53'E, *Halimeda* mats, coral rubble, 1 m, coll. J. Just, September 1984. PARATYPES – NTM W.25295, include 1E, 51 segments, L: 7.40 mm, W:1.1 mm, ovigerous female and 1NE 25 segments, male, location and collection details same as holotype.

Additional (non-type) material examined. NORTHERN TERRITORY: NTM W.23061, 2E, Darwin, Lee Point, *Halimeda* mats on reef, 1 m, coll. C. Watson, September 1984; NTM W.22945*, 2E, Channel Island, 12°33'S, 130°52'E, *Halimeda*, sand and coral rubble, LWS, coll. C. Watson, August 2007; NTM W.23069*, 1NE, 49 segments, W: 1.5 mm, Channel Island, *Halimeda* washings, LWS, coll. C. Glasby, December 2009; NTM W.4062, fragments, 1E, 60 segments, L: 5.5 mm, W: 0.7 mm, Channel Island, *Halimeda*, LWS, coll. C. Watson, December 1986; NTM W.3020, 1E, 53 segments, Channel Island, *Halimeda* and rubble, LWS, coll. P. Alderslade, October 1985; NTM W. 23049, 1E, 88 segments, L: 7 mm, W: 1.7 mm, Nighteliff, algal washings from isolated rocky pools in sandflats exposed on 0.4 m tide, coll. C. Watson, 21 September 2009; NTM W. 13126, 1E, Middle Arm, Darwin Harbour, Stn. 98A, fine sand, 18 m, July, 1993, coll. Marine Ecology Unit; NTM W.02968, fragments, East Point, Fannie Bay, LWS, *Halimeda*, *Caulerpa* washings, coll. C. Watson, October 1985. QUEENSLAND: GBR, AM W.36208, 1, W: 0.6 mm, Lizard Island, between bommies inside entrance to lagoon, corer in sediment, 18 m, coll. C. Watson & A. Jones, October 1978; NTM W.23075*, fragments, Outer GBR, Day Reef, Stn. CGL1016, 14°28'S, 145°32'E, *Halimeda*

Fig. 5. *Treptopale paromolos* sp. nov., NTM W.23049, Darwin, Northern Territory, anterior end of live individual from algal washings in isolated rocky pools on sand flats exposed at 0.4 m tide. Photograph: Chris Glasby.

rubble, 12 m, coll. M. Ekins, April 2008; NTM W.23403*, 1NE, Day Reef, lip of lagoon behind reef crest, CWL1074, 5–10 m, dead *Acropora*, sand and seagrass, coll. L. Avery, September 2010; NTM W.23402*, fragment, Day Reef, CWL1074, reef dropoff, 18 m, coll. S. Smith, September 2010; NTM W.23360, Low Isles, 1 small posterior end, south side drop off, *Halimeda*, algal mat, coral rubble, 6–8 m, coll. C. Watson, December 1987. WESTERN AUSTRALIA: NTM W.2911, fragment, Scott Reef, intertidal reef flat, coral rubble with coralline, green & brown algae, coll. B.C. Russell, August 1984; NTM W.22943*, 1NE, South Scott Reef, middle of western reef, Stn.CWSR-7, 14°08'S, 121°44'E, *Halimeda*, sand, rubble, LWS, coll. C. Watson, October 2008; NTM W.22941*, 1NE, South Scott Reef, southwest corner, Stn.CWSR-6, 14°12'S, 121°47'E, *Halimeda*, sand, rubble, LWS, coll. C. Watson, October 2008; NTM W. 22942*, 1NE, South Scott Reef, southwest corner, Stn.CWSR-6, *Halimeda*, sand, rubble, LWS, coll. C. Watson, October 2008; NTM W.4158, fragments, Ashmore Reef, coralline algae and coral rubble, 15 m,

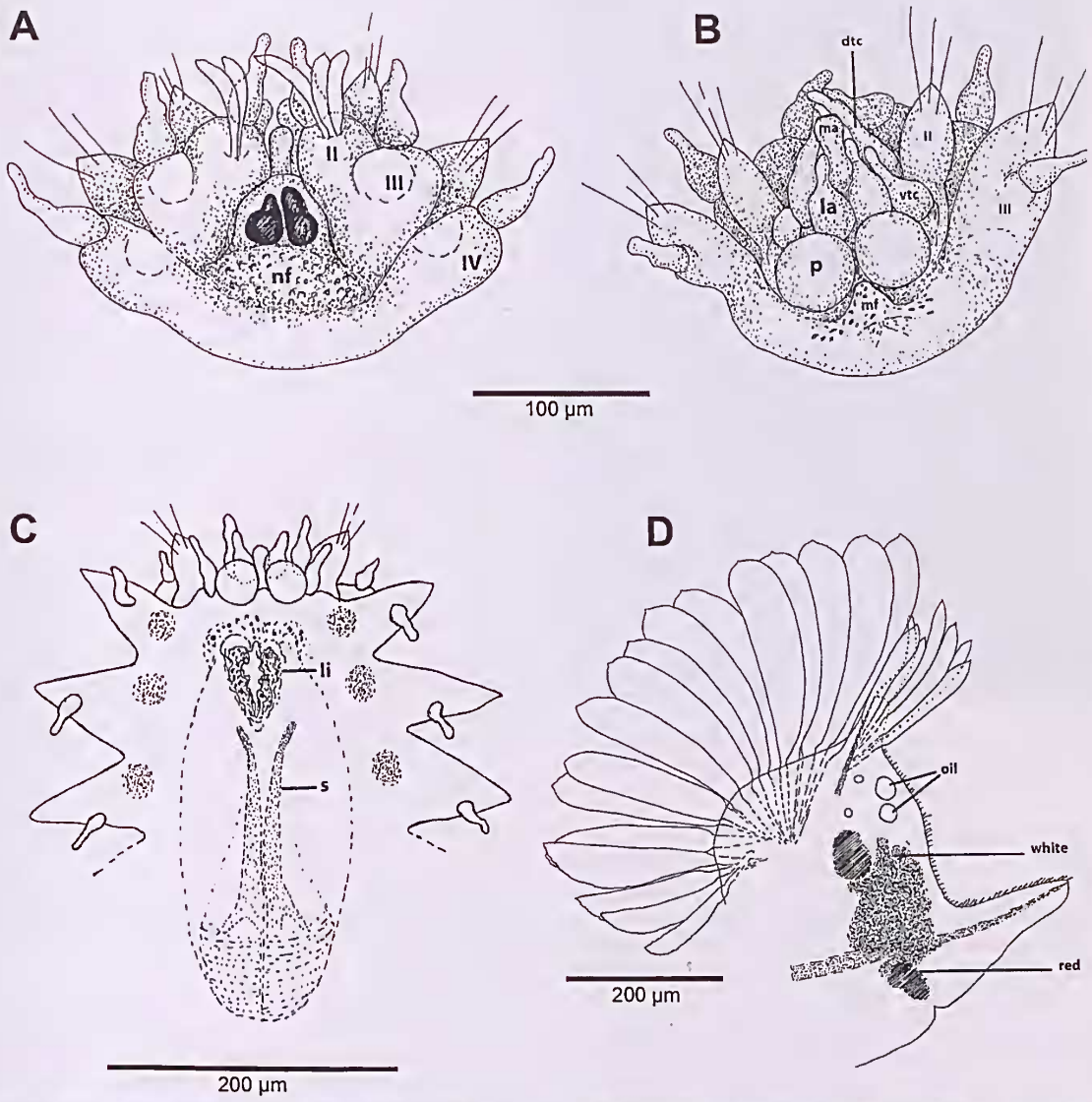

Fig. 6. *Treptopale paromolos* sp. nov., NTM W.02529, Paratype, Darwin, Northern Territory: **A**, anterior end, dorsal view, nf = nuchal fold, II, III, IV segments 2–4; **B**, ventral view, ma = median antenna, la = lateral antenna, p = palps, dtc = dorsal tentacular cirrus segment 1, vtc = ventral tentacular cirrus segment 1; II = segment II (setiger 1), III = segment 3, mf = mouth fold; **C**, NTM W.23049, anterior end, ventral view, li = lips of mouth opening, s = stylets; **D**, NTM W.23049, mid-body parapodium of live individual, oil = oil globules, white = white interramal pigment mass, red = red pigment patches. Scale lines: A – 0.1 mm; B – 0.1 mm; C – 0.2 mm; D – 0.2 mm.

coll. B.C. Russell, February 1984; NTM W.9310, 1NE, ovigerous female, fragments, Ashmore Reef, lagoon patch reef, *Halimeda*, coral rubble, encrusting sponge, 5 m, coll. B.C. Russell, April 1987; AM W.33630, 1, Kimberley coast, Albert Island, Stn. 43, 14°5'S, 124°9'E, rock platform, July 1988, coll. P. Hutchings; AM W.3363, fragments, Kimberley coast, Lucas Island, Stn. 43, 15°2'S, 124°5' E, 30 m, coll. P. Hutchings, July 1988; NTM W.2963, 54 NE, Bedout Island, intertidal reef platform, coral rubble, coll. B.C. Russell, June 1985; AM W.33632, 2NE, Dampier Archipelago, Rosemary Island, Hungerford Bay, 20°49'S, 116°57'E, crevice fauna, 6 m, coll. P. Hutchings, April 1987; AM W.33633,1, ovigerous female, W: 0.8 mm, 1NE, Exmouth, Bundegi Reef, Stn. 391, 21°8'S, 114°2'E, 1–2 m, rocky rubble with coralline algae, green epiphyte, coll. H. Stoddart, January 1984; NTM W. 22992*, 1 NE, Ningaloo, 21°5'S, 113°00'E, Stn. NIN13B, Ningaloo Reef near Tantabiddi, reef slope, coll. N. Bruce, June 2008; NTM W.23367*, 1, ovigerous female, Ningaloo, Stn. CWNR10-011, 12 m, ARMS artificial settling plates, May 2010. WESTERN PACIFIC OCEAN. NEW GUINEA: NTM W.21784, 1, 40NE, Madang, Reef inside Ras Passage, 5°10'S, 145°50'E, Stn. RH91/94B, coral

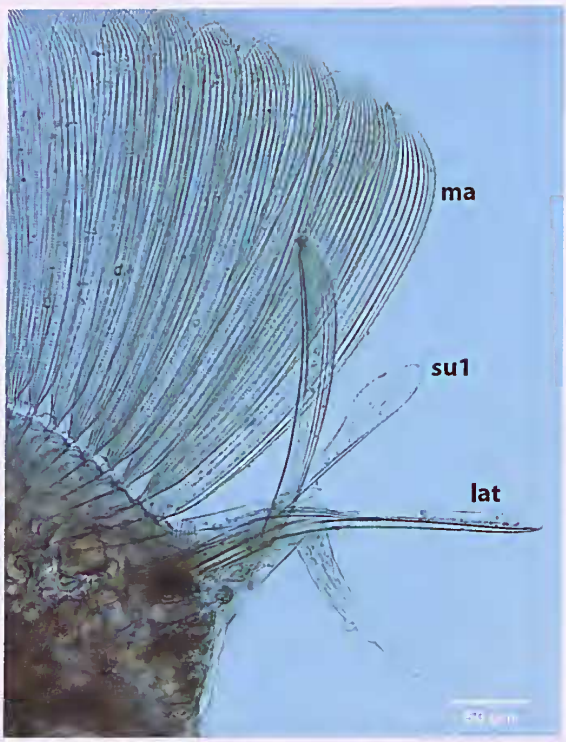

Fig. 7. *Treptopale paromolos* sp. nov., NTM W.21784, Madang Reef inside Ras Passage, Papua New Guinea, slide preparation mid-body notopodium in part, lat = lateral paleae, su1 = subunit 1 palea, ma = main paleae group.

reef, 14 m, coll. J.R. Hanley, October 1994. INDONESIA: NTM W.21789, fragments, Flores, Maumere, Halimeda, red algae, 3–6 m, coll. B.C. Russell, November 1991. PHILIPPINE ISLANDS: NTM W.13168, fragments, Luzon, Cape Bolinao, 16°25'N, 119°50'E, coral rubble, sponge, red algae, 12–25 m, coll. B.C. Russell, October 1995. PALAU ISLANDS: USNM 1076942, fragments, Iwayama Bay, 7°19'N, 134°29'E, eel grass, algae, sand and coral flat, coll. F.W. Bayer, July 1955. INDIAN OCEAN. THAILAND: NTM W.232261, 59E, Similan Island, 9°N, 98°E, dead *Acropora*, coll. A. Natcewathana & J. Hylleberg, January 1981. SRI LANKA: NTM W.23361, fragments, Galle, 6°04'N, 80°09'E, reef flat beneath lighthouse, *Halimeda*, coral rubble, fine sand, 0.5 m, coll. B.C. Russell, October 1991. POST-LARVAL/JUVENILE MATERIAL: NTM W.23062, 10E, length 2.04 mm, width 0.84 mm, Western Australia, Ashmore Reef, 12°44'S, 122°59'E, sand coral rubble, patches *Porites* microatolls & seagrass, fine leafed *Halimeda* in clumps, 1 m, coll. H. Larson, August 1986; HZM P. 16717, 1 NE (original description 14E), L: 0.8 mm, W: 0.4 mm, Port Hedland, coarse sand flats at estuary mouth of Pretty Pool, coll. Hartmann-Schröder, September 1975.

Description. Body pale yellow-white, with silvery to very pale golden paleae covering dorsum (Fig. 5). Long, quadrate-shaped prostomium with 2 pairs fused dark maroon-red eyes, median antenna short, distally bulbous, 2 filiform lateral antennae with bulbous bases, 2 rounded palps. Prostomium contracted between 2 anterior segments, covered posteriorly by small nuchal fold (Fig. 6A,B). Mouth fold triangular, small, with scattered brown pigment spots immediately below palps near segment 3 boundary; pharynx with 2 slender stylets, pale yellow with brown distal tips (Fig. 6C).

Segment 1 uniramous, achaetigerous with 2 pairs of tentacular cirri. Segment 2 (setiger 1) biramous; notopodia with 3–4 short, slender paleae with 7 ribs and dorsal cirrus; neuropodia with faseicle of spinigerous chaetae, ventral cirri absent (Fig. 6A,B). Segment 3 (setiger 2) notopodium with 1 lateral palea, 1 subunit one palea, 12 main paleae; latter short, symmetrical, distally broad with 8–10 ribs and raised ribs. Median paleae absent, first present about segments 4 to 5.

Mid-body notopodium with 2–4 (6) slender, subacicular lateral paleae with 5–8 (9) ribs with fine serration on both margins. Shorter, more fragile, subunit 1 paleae overlying dorsal acicula with pinched, asymmetric inner margin (Figs 7, 8E). Symmetrical main paleae number 10–15 (18,20) with 17–21 (23) ribs with none to 3–4 lightly ornamented raised ribs (Figs 7, 8E). Lateral and medial main paleae slightly more rounded distally and mid main slightly broader. Asymetrical 3–4 (5) median paleae present with 10–13 (15) ribs with hardly visible 1–3 lightly beaded ribs or slightly more robust with 3–5 ribs raised (Figs 6D, 8A).

Anterior-most neuropodia with spinigers and long bladed falcigers. By segment 5, neuropodial superior spinigers drop out and replaced by 2 superior long bladed falcigers. Mid-body neuropodium with 3 superior long bladed falcigers, 3–4 less long bladed falcigers, 10–15 medium bladed falcigers and 4–8 inferior short bladed falcigers (Fig. 8D). Pygidium quadrate with 2 slender anal cirri (Fig. 8B).

Intraspecific variation. An entire specimen of *T. paromolos* from Darwin with 41 segments was dissected to observe its chaetal types, especially lateral and subunit 1 paleae, down the body. Shorter and squarer, more heavily ornamented main paleae are evident in anterior setigers, as seen in *T. homalos* (Fig. 3B), becoming much less ornamented after setiger 5 and decreasing in ornamentation almost entirely down the body. The anterior five setigers showed a typical mixture of juvenile transition and adult paleae with fully adult paleae types at setiger 6.

Subunit 1 paleae are present from setiger 6 throughout the body to setiger 40 and an occasional notopodium has two subunit 1 paleae. The laterals increase in number from setigers 10 to 15, with the mid-body setigers 20 to 26 exhibiting even larger numbers. As noted for *T. homalos*, a few random notopodia had larger numbers of lateral paleae (e.g. setiger 12 possessed one notopodium with 6 laterals plus a few spines; the corresponding notopodium had 3 laterals). Small anterior spines, of the type seen in the *T. rudolphi* specimen from Florida, are very infrequent,

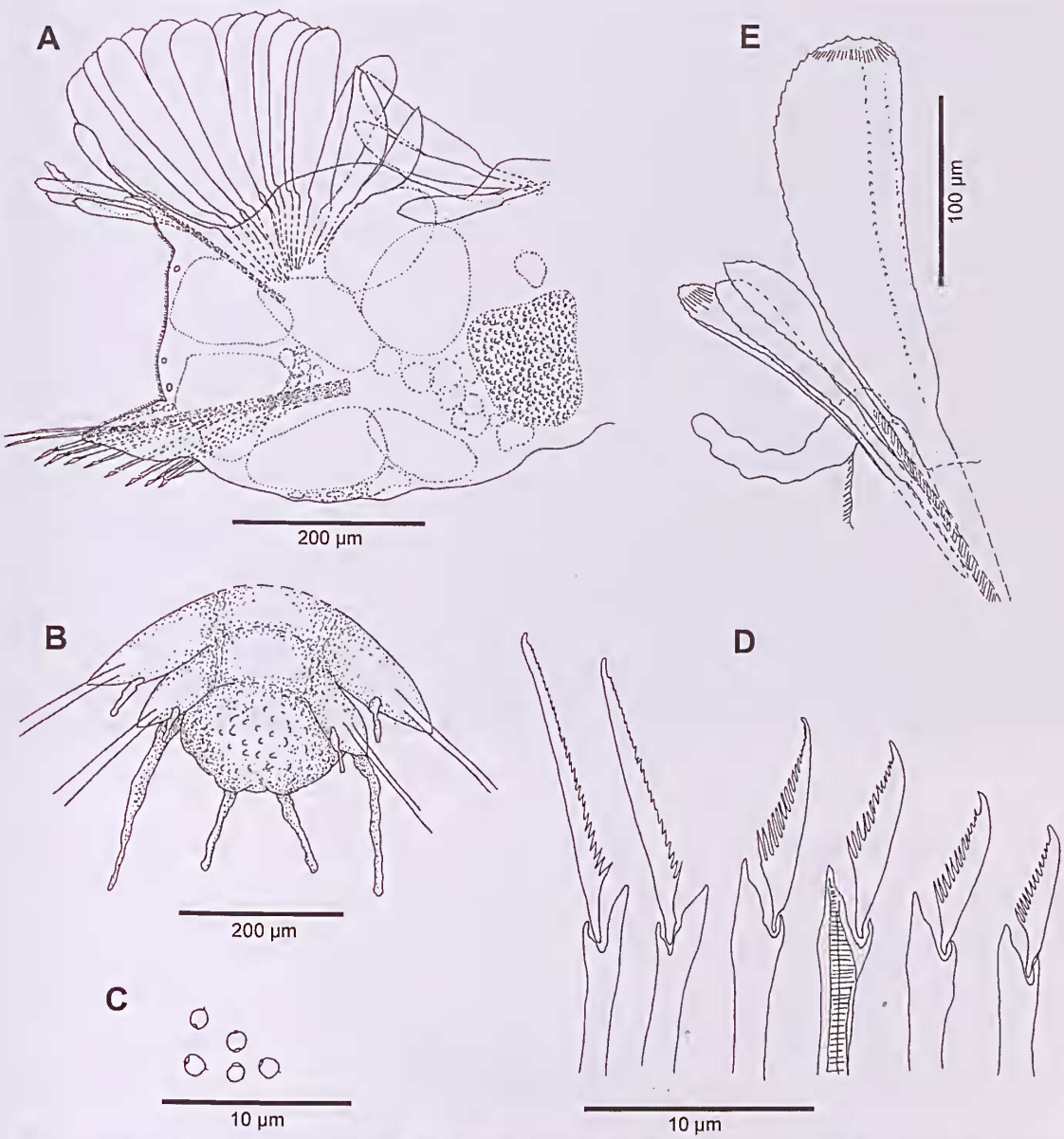

Fig. 8. *Treptopale paromolos* sp. nov., **A**, Holotype, NTM W.23048, Lee Point, Darwin, Northern Territory, female with large eggs, mid-body parapodium; **B**, Paratype, NTM W.2529, pygidium; **C**, Paratype, NTM W.2529, Lee Point, Darwin, Northern Territory, sperm; **D**, Paratype, NTM W.2529, Lee Point, Darwin, Northern Territory, neuroehaetal types from mid-body neuropodium – superior long faleiger, mid-superior long faleiger, middle faleigers, inferior short faleiger; **E**, NTM W.23361, Sri Lanka, mid-body notopodium in part figuring lateral, subunit 1 and lateral-most main paleae. Scale lines: A – 0.2 mm; B – 0.2 mm; C – 0.01 mm; D – 0.01 mm; E – 0.1 mm.

and are no doubt larval remnants (see spine in juvenile, Fig. 9C). Within the last 10 chaetigers the laterals become fewer with fewer ribs.

Largest numbers of main paleae occur mid-body at the greatest width of the body. In the dissected individual the main paleae overall are fragile and mid-body setigers showed 1–2 medial-most main paleae comparatively more slender and more distally pointed with fine, dense ribs (Fig. 8A). Median paleae anterior to about setiger 10 have three typical broad juvenile paleae, with the mid-body possessing four adult median paleae and an occasional notopodium with five adult median paleae. Within the posterior 10 setigers, median numbers become less and the two medial-most median are small and slender. All main and median paleae have a typical fine 'broken line' raised ribs. It is interesting to note this *T. paromolos* specimen had two anterior notopodia exhibiting the larger *T. homalos* type subunit 1 palea. This has also been observed very

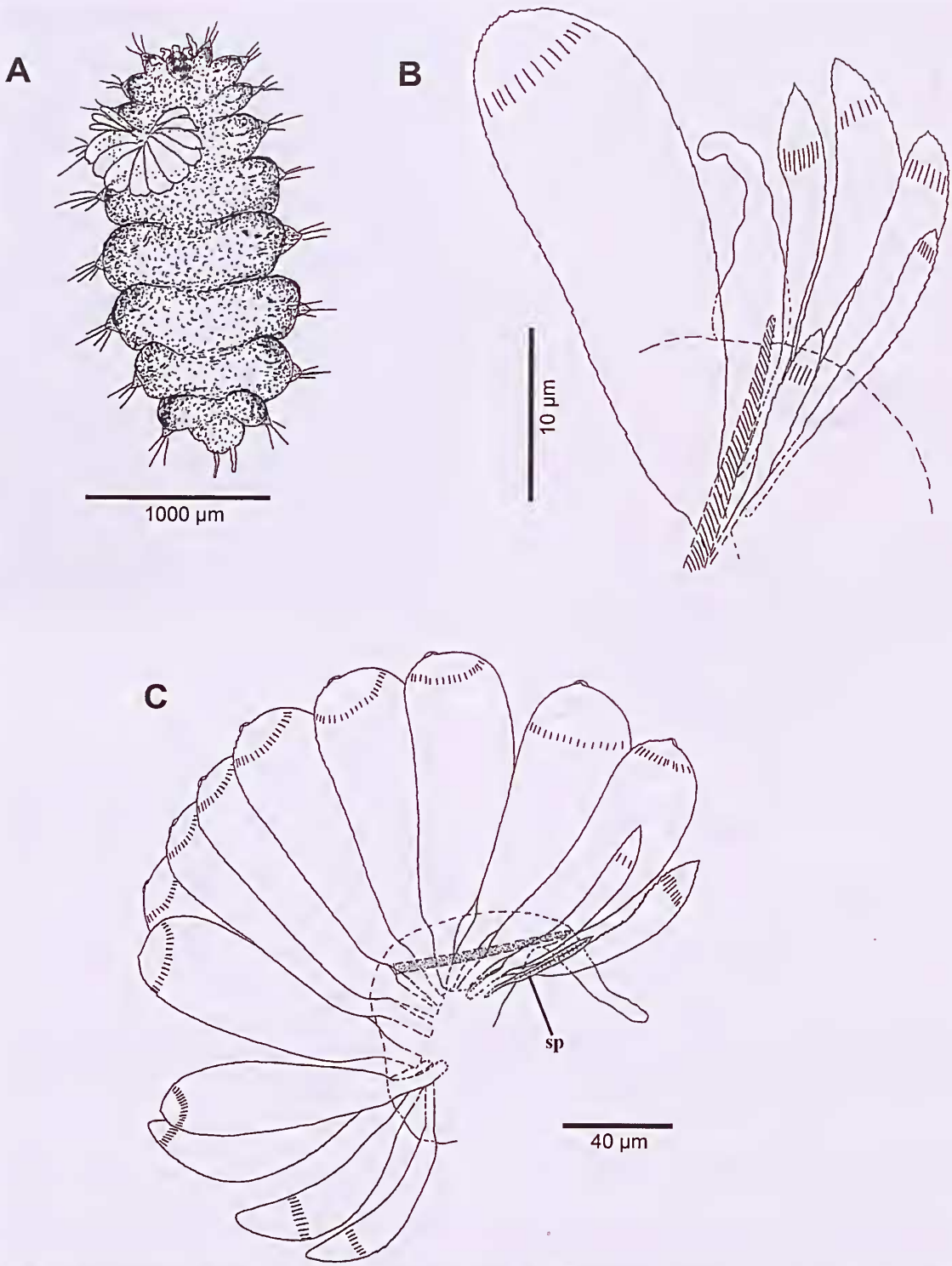

Fig 9. *Treptopale paromolos* sp. nov., **A,B**, NTM W.23062, Ashmore Reef, Western Australia: **A**, 10E post larva; **B**, detail of notopodium of setiger 6; **C**, HZM P.16717, Port Hedland, Western Australia, notopodium of setiger 11(14 E). Scale lines: A – 1.00 mm; B – 0.01 mm; C – 0.04 mm.

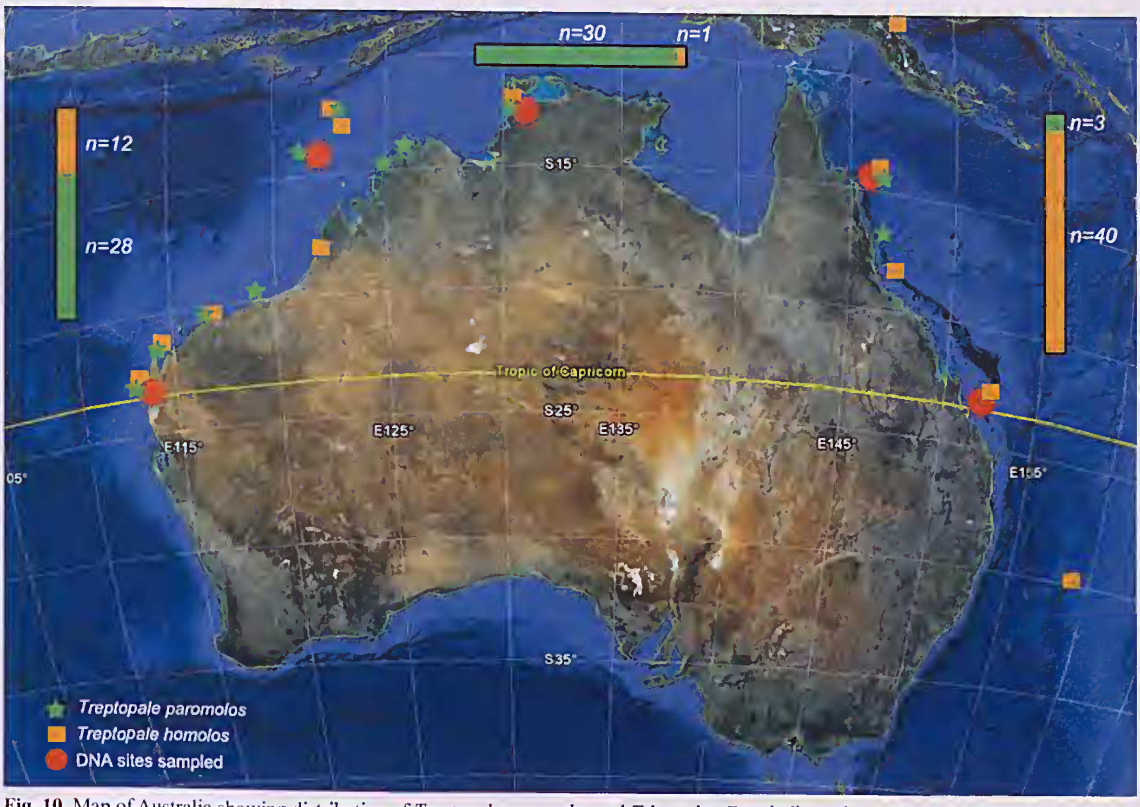

Fig. 10. Map of Australia showing distribution of *Treptopale paromolos* and *T. homalos*. Bars indicate the number of individuals of each species collected within the different regions, defined as: Eastern coast = Elizabeth Reef to Lizard Island; Northern coast = Darwin region; Western coast = Kimberley region to Ningaloo.

infrequently in one or two setigers in anterior ends of other *T. paromolos* specimens.

Intraspecific differences observed included a number of larger specimens from Western Australia (Bedout Island, Ningaloo) that possessed the highest numbers of main paleae and numbers of ribs (see numbers in brackets in species description).

Description of post-larvae (Fig. 9A,B). Yellowish body with brownish pigment patches on anterior edges of notopodia, transparent paleae fans cover dorsum. Anterior 5 setigers tapered; body segments broadest and deepest at setigers 6 and 7, narrowing thereafter with clear segmental lines. Body puffed up with pale yolk granules; oil globules present in neuropodia (Fig. 9A). Prostomium with 2 large pairs of red eyes, bulbous median antenna, pair of lateral antennae and ventral ovate palps. Segment 1 with pair of dorsal and ventral tentaeular cirri and segment 2 (setiger 1) with dorsal cirri, no ventral cirri. In dorsal view, 2 tiny stylets visible below glandular nuchal fold which is posterior to prostomium, extending to segmental line of setiger 3.

Setiger 1 with 5 typically short, 'lateral-type' paleae with 3–5 ribs. Setiger 2 with more transitional paleae types, inserting in circle formation, with 1–2 broad lateral and slender main plaeae with 8–11 ribs and 6–8 raised ribs. Asymmetric median paleae rounded distally with 8 ribs all raised.

Increasing adult paleal types from setiger 3, inserting in horizontal ridge with 3 lateral and 6 main plaeae with 12–13 ribs and about 5 raised ribs; median paleae broadly asymmetric with 8–10 ribs, about 3–4 raised. Setiger 6 exhibits classic adult types: 4 lateral pálaea with 4–7 ribs and adult subunit 1 palea with 8 ribs, plus main with 13 ribs and very lightly ribbed (Fig. 9B). Posterior setiger 9 has 3 slender lateral with 3–6 ribs plus 1 subunit 1, palea with 7 ribs; 1 main with 16 ribs and very lightly 4–5 raised ribs; 2 small slender median with 3 and 6 ribs.

Setiger 1 has spinigerous neurochaetae and setiger 2 has long-bladed falcigers. Adult type falcigerous neurochaetae present from setiger 3 and adult inferior falcigers with broad short blades present from setigers 5–6. Neurochaetae of setigers 8–9 all slender.

Description of juvenile. Nuchal area glandular but no discreet nuchal fold seen. Setiger 1 with 3 short 'lateral' type paleae with 3–6 ribs; setiger 2 with similar laterals plus main paleae with 13 ribs; typical juvenile broad median with 7–8 ribs. Mid-body has 7–9 main with 14–16 ribs. Setiger 11 possesses 1 small lateral spine with 2 ribs and serrated margins and 1 lateral plus typical adult subunit 1 palea with 7–8 ribs; 2 broad type median with 9–10 ribs

(Fig. 9C). Neuroehaetae mid-body with typieal superior long-bladed faleigers and inferior short-bladed faleigers. Mid-superior group, medium length bladed faleigers with particularly long basal serrations (Hartmann-Sehröder 1979: 160, fig. 13).

Remarks. In addition to the distinetive asymmetrie subunit 1 palea and much less raised rib and paleal marginal serrations, *Treptopale paromolos* possesses paler paleae, the body has a reetangular eross seetion, and the paleal fans sit flatter on the dorsum.

Paleal types of setigers 1 and 2, paleal insertion pattern, transitional notoehaetal types plus main paleae with greater number of raised ribs within the anterior five setigers, seen in post-larval material, are retained in adults of both *Treptopale* speeies. The retention of more ornamented paleae plus the rare oeeurrenee of *T. homalos* subunit 1 type palea, within the anterior five most eonservative setigers of *T. paromolos,* illustrates its elose relationship with *T. homalos.*

Habitat and Distribution. *Treptopale paromolos* is often found amongst eoral rubble on muddier sands of intertidal reef flats, from sand and seagrass flats and eoral rubble assoeiated with *Halimeda* algae, eorallines and enerusting sponges from LWS to 30 m. It is presently known from Sri Lanka and from loealities along the rim of the western Indian Oeean, from Thailand to the eoast of tropieal Western Australia. In the western Paeifie Oeean, *T. paromolos* is present from the Palau Islands to New Guinea and the tropieal eoasts of northern and eastern Australia.

Both *Treptopale* speeies oeeur sympatrieally in eolleetions from the Philippines and they also eo-oeeur in the same areas of Indonesia and Thailand. At present it is not known whether the absenee of *Treptopale paromolos* from the wider western Indian Oeean and eastern Paeifie range of *T. homalos* is due to laek of speeifie habitat eolleeting.

Etymology. The speeies name *paromolos* is a noun in apposition from the Greek meaning 'nearly equal' and refers to the pineh ed, asymmetrie inner margin of the sub unit 1 palea.

REPRODUCTION AND DEVELOPMENT IN *TREPTOPALE*

Treptopale has separate sexes whieh are illustrated in this paper. Individuals possess typieal glandular swollen rod-like internal struetures posterior to the dorsal eirrus, as in all mature paleate ehrysopetalid speeies (Perkins 1985, Watson Russell 2000a).Within the parapodia of mature males of both *Treptopale homalos* and *T. paromolos* are large eream-eoloured saes that eontain very small ovoid to rounded sperm, some observed with minute tails (Fig. 8C). The sperm is not to be eonfused with similar-sized elongate white pigment granules (whieh appears as a dark greyish mass under a compound mieroseope) present between the rami in gametogenie male and female individuals (Fig. 6D). Thousands of these granules ean be seen spilling out of the planktonie speeimens of *T. homalos* that also earry sperm. The funetion of these white granules is unknown.

Samples overall had small numbers of females with mature eggs. *Treptopale paromolos* females from populations in Ningaloo and Darwin possessed mature eggs (both with a size range of 130–200 µm), with latter individuals having about eight per mid-body parapodium (Fig. 8A). These large eggs, with the nueleus just visible, as well as smaller eggs (40 µm) that oeeur in the same parapodia have a very granular surfaee. The small eggs appear to be made up of many smaller ones, referred to as an egg 'paeket' with no nueleus visible (as eompared with *Arichlidon*, Watson Russell 1998). Three *T. paromolos* females were observed to have large eggs in elusters on the ventrum. It was diffieult to aseertain whether these elusters had been extruded by the female when it was eolleeted or they were an attaehed brood. Slide preparations show enhaneed glandular strueture along the ventral parapodial edge, posterior to the ventral eirrus. Ultrastruetural studies are needed to aseertain whether the eggs are brooded.

Mature females of *Treptopale paromolos* from populations from Ashmore Reef and Madang possessed notopodia and neuropodia staeked full of small eggs (size range of 20–30 µm) with a granular surfaee and numbering 200 plus per mid-body parapodium (Fig. 7). Mature females of *T. homalos* predominantly had 'paeket' type eggs measuring 40–60 µm. One individual from Exmouth had eggs (80–120 µm) with elear nuelei numbering about 40 per parapodium. Only one *T. homalos* speeimen, from Lizard Island, with the identifiable subunit 1 palea and ornamented main (referred to as an atypieal in the speeies diseussion), had large eggs (120–150 µm) in a eluster on the ventrum.

Assuming that small numbers of large eggs in elusters indieates leeithotrophy and very numerous smaller eggs indieates planktotrophy, the above data shows that either different reproduetive modes are employed within *Treptopale paromolos* and *T. homalos* or that more than one speeies is aetually present within these presently defined morphologieal units.

Benthie post-larval individuals of 10 segments display main paleae similar to an adult and their gut is filled with yolk. Oil globules evident in the larvae (Fig. 9A) are also retained within the parapodia of adults (Figs 6D, 8A). Oil globules may be small or large and seep out in yellow globules from laeunae in broken segments. Live individuals may also possess within their parapodia bright yellow and orange, as well as white, pigment pateh es (Fig. 6D). The former is referred to as an "internal eavity eontaining elear substanee, perhaps oil" and the latter as "glands eontaining opaque granules" by Perkins (1985: 907) for *T. rudolphi*. Oil globules are also present in parapodia of adult *Paleanotus* but appear absent in other ehrysopetalid genera (pers. obs.).

Males of *Treptopale homalos*, found in mid-water, possess no aeeessory ehaetae as doeumented for speeies of *Arichlidon* reported from the plankton (Watson Russell 1998,

2000a). The retention of oil globules in adult *Treptopale* may enable individuals to rise up and maintain stability within the water column. *Treptopale* species also have large, broad segments in the mid-body that break apart like pieces of a jigsaw puzzle, observed also in *Thraumastos* living at abyssal depths at hot vents and the only other chrysopetalid genus exhibiting extreme fragmentablity (Watson 2001). Body fragmentation is allied with a benthic and mid-water behaviour that includes jettisoning of segments under stress.

Treptopale homalos adults have been reported from mid-water (Watson Russell 2000a, this paper) but no *Treptopale* early larval stages have been found in the plankton. Species that show wide distributions are either old species that have time to take advantage of emerging stepping stones during low sea level stands, or species that have long larval stages (Hoeksema, 2007). There is no evidence as yet that *Treptopale* possess free-living larvae capable of long distance dispersal.

OCCURRENCE AND HABITAT OF *TREPTOPALE* IN NORTHERN AUSTRALIA

At present there appears no latitudinal species pattern between inshore and offshore reefs or longitudinal north-south differences based on morphology. *Treptopale homalos* appears to be the predominant *Treptopale* species on the eastern Australian coast. Material has been examined from over 40 collecting sites from Queensland offshore islands and reefs and mainland fringing reefs from the southern and northern Great Barrier Reef and from four different sites around Madang, Papua New Guinea, comprising over 60 individuals (Fig. 10). *Treptopale homalos* has been collected from two sites at Elizabeth Reef atop submerged volcanic sea mounts, lying at the southern boundary of the Coral Sea at 29°S. Single specimens of *Treptopale paromolos* have been collected from three sites on the the north-east Australian coast and one site from Madang in rubble and silty sand habitats. *Treptopale paromolos* and *T. homalos* occur sympatrically at one site, Day Reef, on the Outer Barrier, GBR.

The largest populations of *Treptopale paromolos* are inferred to occur in northern Australia, predominantly from silty reefs in Darwin Harbour, Northern Territory with over 40 individuals counted. Only one individual of *T. homalos* has been found in the same Darwin collection as *T. paromolos* in a habitat of *Halimeda*, coral rubble, brown and red algae on a silty reef at LWS (Fig. 10).

Both species of *Treptopale* are present on the offshore and mainland reefs off northern Western Australia with no particularly clear pattern, although *T. paromolos* is slightly more common. *Treptopale homalos* represents 12 specimens from six sites and *T. paromolos* 28 specimens from nine sites. Both species occur sympatrically at three of these localities (Fig. 10). *Treptopale paromolos* and *T. homalos* co-occured in a very large sample of coral rubble with coralline algae, sponge, soft coral and tunicate growth from Ashmore Reef, Timor Sea. The former species appeared in three subsequent trips to Ashmore Reef, including sand and seagrass habitats, whereas *T. homalos* turned up from Cartier Island just to the south of Ashmore Reef. Further south, the massive coral banks of Scott Reef on the edge of the continental shelf have had six sites visited over a period of 26 years and all visits resulted in only *T. paromolos* being collected. *Treptopale homalos* and *T. paromolos* are both found from the Western Australia mainland and nearshore island reefal sites from the northern Kimberley coast to Ningaloo at 21°S (Fig. 10). Both species are present in coarse coral rubble, with the latter also found with coralline algae on intertidal reef platforms and from coarse sand flats at the mouth of estuaries.

At present there is some evidence that reproductive isolation is maintained by habitat partitioning for these two species (see above) which co-occur within a reefal environment and inhabit a similar depth range. *Treptopale paromolos* has been reported from finer sediments from the deeper lagoonal sediments of Lizard Island, predominance among the silty rubbles of Darwin and offshore north western Australian shallow reefs of sand and seagrass habitats. *Treptopale homalos* is most common amongst coral rubbles of the less sedimentary, deeper, clearer water reefs of the GBR.

DISCUSSION

The biogeographic distribution of a species is intrinsically linked to its developmental mode, habitat preference, and geological and climatic history. The presence of *Treptopale rudolphi*, *T. homalos* and *T. paromolos*, three morphologically very closely related species, within a pantropical belt including sympatric distribution of the two latter two across the Indo-Pacific Ocean, is indicative of a geologically old species complex. Although it appears adults have the ability to rise up in the plankton, the absence of a planktonic larval stage sugests even more strongly that these present species represent lineages derived from an ancestor that evolved within a shallow water Tethyan fauna present before the Cenozoic. This uniform pantropical fauna was disrupted by a series of plate tectonic events in the early Miocene (approx. 20 million years ago, with the collisions of Africa/Arabia with Europe and Australia/New Guinea with Indonesia) and the Middle Miocene (rise of the Central American Isthmus). The isolation of continents, reorganisation of oceanic circulation systems and imposition of a steep latitudinal gradient led to effective barriers for migration and subsequent speciation within two main tropical foci – the Indo-West Pacific and the Atlantic-Caribbean-East Pacific (Crame & Rosen 2002).

Much more recently, over the past 130,000 years, sea levels associated with glacial cycles have profoundly modified the Australian shallow water reefal systems. Levels

dropped to 120 m below present sea level around 18,000 years ago, with the result of isolating Australia's north-eastern coast from the west due to the closure of Torres Strait (Choat & Russell 2008). The loss of the emergent coral reefs on the Australian continental shelves and also the fringing reefs throughout the western Pacific island chains meant that coral communities had to move downwards with descending sea levels along relatively steep continental or volcanic island margins to survive (Potts 1984). Water exchange between the Pacific and Indian Oceans became obstructed due to narrower and shallower sea passages and the amount of freshwater runoff and suspended sedimentation increased. These conditions and the emergence of physical barriers led to isolated, disconnected populations which may have caused subsequent speciation (Hoeksema 2007).

During the Pleistocene, reef corals remained in fringing reefs in eastern Indonesia along the edge of the Sunda Shelf, in northwestern Australia along the Sahul Shelf and in eastern Australia along the outer barrier at the edge of the continental shelf. Rapid sea-level rise in the Holocene, 18 to 6 thousand years ago, led to inundation of continental shelves and re-establishment of coral communities by organisms with planktonic larvae and adult movement (Hoeksema 2007). Potentially the organisms colonising these available areas would constitute both relict species that were able to survive in reefal open refuges during glaciation as well as new species that had evolved as a result of disruption to the range of an ancestral species. The present distribution of *Treptopale homalos* and *T. paromolos* across northern Australia begs a number of questions. A first scenario postulated is that of the two morphological forms, *Treptopale homalos* and *T. paromolos,* evolved from a common ancestor that had a widespread western Pacific and Australasian distribution long before the Pleistocene. The change in physical conditions and emergence of barriers (e.g. closure of Torres Strait during the last glacial maximum) would have separated existing northern Australian populations of *Treptopale homalos* and *T. paromolos*. Speciation may have then taken place without phenotypic differentiation. The sympatry of the two species evident today is a reflection of *in situ* lineages that recolonised substrates after deglaciation on the east and west Australian coasts and with probable secondary colonization subsequently.

Another scenario postulates that *Treptopale paromolos* evolved during the glacial period in response to the greater sedimentary conditions of shallow seas of the Arafura and Sahul Shelf by, for example, selection of minimal paleae ornamentation. The conditions of freshwater runoff and suspended sedimentation, present in the Pleistocene, are still apparent today in areas of the Sahul Shelf, Java and Arafura Seas (Hoeksema 2007). The presence of *T. paromolos* currently along the northern and northwestern Australian silty coasts could reflect *in situ* lineages that may also include secondary recolonisers.

Ongoing phylogenetic analyses of *Treptopale* (Watson in prep.) and DNA studies (Wei & Watson in prep.) will no doubt prove useful in sorting out these scenarios.

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